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French, A.S.; Snyder, A.W.; Stavenga, D.G.

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Image Degradation by an Irregular Retinal Mosaic

A. S. French*, A. W. Snyder, and D. G. Stavenga**

Departments of Neurobiology and Applied Mathematics, Institute of Advanced Studies, Australian National University, Canberra, Australia

Abstract. In order to understand the significance of a regular photoreceptor mosaic we quantify the effect of deviations from regularity. Such deviations are shown to cause a deterioration in the quality of the image at the photoreceptor level because of image demodulation and image distortion. Consequently, a regular receptor array is necessary for extracting all of the spatial information available in the retinal image.

Introduction

The spatial information contained in a visual signal is successively reduced as the signal passes through the various stages of a visual system. First, optical abberations and diffraction at the pupil limit the optical quality of an eye and act as low-pass spatial frequency filters (Rodieck, 1973). Second, the finite width of the photoreceptors results in a further loss of high spatial frequencies (Snyder et al., 1976). Third, the spacing of the photoreceptors sets an upper limit to spatial resolution as formulated by the sampling theorem (Snyder and Miller, 1977). When the angular separation of the photoreceptors is $\Delta\phi$ the maximum spatial frequency which can be unambiguously resolved by a one-dimensional array is $v_s = 1/2\Delta\phi$. The sampling theorem in its classic form assumes that the array of photoreceptors is uniformly spaced. A regular organization of the retina is common, especially in the eyes of animals which rely heavily upon vision, but irregularities do occur in photoreceptor mosaics (Engström, 1963; Rodieck, 1973).

* *On leave from:* Department of Physiology, University of Alberta, Edmonton T6G 2H7, Canada

** *On leave from:* Biophysical Department, Laboratorium voor Algemene Natuurkunde, Ryksuniversiteit Groningen, Westersingel 34, Groningen, The Netherlands

Requests for reprints should be sent to Dr. French at the University of Alberta

In order to understand the importance of a regular photoreceptor mosaic we quantitatively consider the effects of deviations from regularity. We show that irregularity causes an additional loss in spatial information, in that the modulation transfer (signal amplitude) decreases and random noise is added to the signal. We derive these results analytically for an infinite array with infinitely small spacing between the photoreceptors. We then compare the predicted information processing capacity with that of a computer simulated finite array with finite photoreceptor spacing.

Spatial Sampling in an Infinite Array

Consider a sinusoidal spatial intensity distribution which is sampled by a unidimensional array of photoreceptors. When the array is regular its ability to reconstruct the spatial intensity distribution is given by the modulation transfer function:

$$\begin{aligned} M(v) &= 1 \qquad v < 1/2\Delta\phi \\ M(v) &= 0 \qquad v > 1/2\Delta\phi \end{aligned} \tag{1}$$

where v is spatial frequency, ϕ is a spatial dimension, and $\Delta\phi$ is the interreceptor separation. Thus only spatial frequencies up to the sampling frequency $v_s = 1/2\Delta\phi$ can be reconstructed without error (Snyder and Miller, 1977).

In order to generate an irregular array of photoreceptors we allow each photoreceptor to be perturbed from its regular position by a random perturbation. The random perturbation is assumed to be gaussian with a mean of zero and a standard deviation of ϕ_p. Inspection of Figure 1 shows that the amplitude of the sampled sinusoid must now be diminished if the average value of the signal at a series of random points around each regular photoreceptor is taken. This diminution in amplitude is maximal when the regular position of a photoreceptor is at the peak of a wave

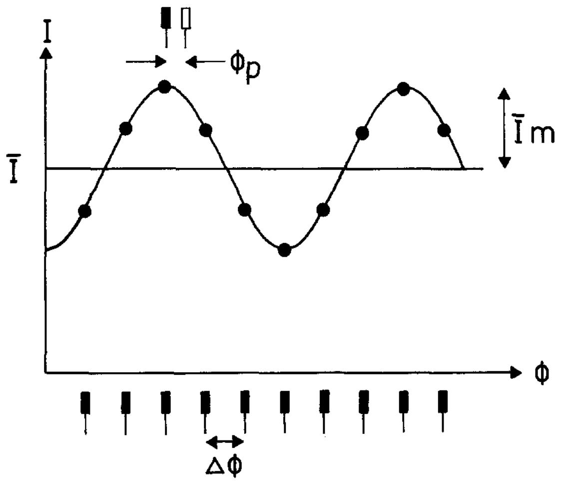

Fig. 1. Sampling of a sinusoidally varying spatial light distribution by a regular array of photoreceptors. The light intensity at a point in space, ϕ, is given by $I=\bar{I}(1+m\cos(2\pi\nu\phi))$, where $\bar{I}$ is mean light intensity, m is modulation depth, and ν is spatial frequency. The interreceptor spacing is $\Delta\phi$. Irregular arrays of photoreceptors have the same mean spacing but are perturbed by a gaussian process of standard deviation ϕ_p

since movement in either direction away from the peak produces a smaller sample. The minimum effect occurs at the point of inflection where the sampled value is zero.

An estimate of the expected decrease in amplitude may be obtained by the following approximate argument. Let the value of the modulation at some position, ϕ, be:

$$x(\phi)=\cos(2\pi\nu\phi). \tag{2}$$

Now let this position be deviated by a small perturbation $\pm\phi_p$. The average sampled value is then given by:

$$\begin{aligned}\bar{x}_p(\phi)&=\tfrac{1}{2}[\cos(2\pi\nu(\phi+\phi_p))+\cos(2\pi\nu(\phi-\phi_p))]\\&=\cos(2\pi\nu\phi)\cos(2\pi\nu\phi_p)\\&=x(\phi)\cos(2\pi\nu\phi_p).\end{aligned} \tag{3}$$

In Appendix A the result of (3) is proved rigorously for a regular array in which each photoreceptor is perturbed by a white gaussian process of standard deviation ϕ_p and zero mean, and the sampled values are treated as if they had arisen from a regular sampling process. Since the input function $x(\phi)$ is attenuated on average by the factor $\cos(2\pi\nu\phi)$, the mean modulation transfer function (for $\nu<1/2\Delta\phi$) is given by:

$$\overline{M(\nu,\phi_p)}=\cos(2\pi\nu\phi_p). \tag{4}$$

In addition to the loss in signal, resulting from the perturbations to the array, a second effect occurs. Since the irregularly sampled signal is no longer a pure sinusoid there are spatial frequencies introduced into the sampled signal which were not present in the original sinusoid. These other spatial frequency components will constitute a noise signal which is not correlated with the original modulation signal.

The variance of a sinusoid of unit amplitude is $\frac{1}{2}$, and in the case where the independent variable is subjected to a gaussian perturbation the variance of the randomly sampled sinusoid is similarly $\frac{1}{2}$, as is shown in Appendix B. We have shown above that the amplitude of the original spatial frequency component in the irregularly sampled signal is $\cos(2\pi\nu\phi_p)$ so that the variance of the noise component must be given by:

$$\tfrac{1}{2}-\tfrac{1}{2}\cos^2(2\pi\nu\phi_p)=\tfrac{1}{2}\sin^2(2\pi\nu\phi_p).$$

The mean amplitude of the noise component is therefore:

$$\overline{N(\nu,\phi_p)}=\sin(2\pi\nu\phi_p) \tag{5}$$

and so the mean signal to noise ratio is given by:

$$\begin{aligned}\overline{M(\nu,\phi_p)}/\overline{N(\nu,\phi_p)}&=\cos(2\pi\nu\phi_p)/\sin(2\pi\nu\phi_p)\\&=\cot(2\pi\nu\phi_p).\end{aligned} \tag{6}$$

Sampling in a Finite Retinal Array

Real retinal arrays are not extended into infinity and do not have infinitely closely spaced receptors. To investigate sampling in a finite array we performed a computer simulation by taking a (unidimensional) array of 100 samplers with angular spacing $\Delta\phi$, which we assumed to view a series of sinusoidally varying spatial light distributions having unit modulation and spatial frequencies from 0 to $\nu_s=1/2\Delta\phi$, in steps of $\nu_s/50$. The positions of the samplers were then randomly shifted by the addition of a series of gaussian distributed random numbers. The random numbers were generated from a sequence of uniformly distributed random numbers (Hamming, 1962) and had zero mean and a specific standard deviation ϕ_p. The value of the sample was then computed at each of the randomly shifted positions.

The series of sample values was processed by the discrete Fourier transform (Newland, 1975) as if the samplers had been equally spaced. The process was then repeated ten times for each spatial frequency and standard deviation. To compute the amplitude of the observed signal at the input spatial frequency the average power in the resultant spectrum was used:

$$\overline{M(\nu,\phi_p)}=\left(\frac{1}{10}\sum_{n=1}^{10}(a_\nu^2+b_\nu^2)\right) \tag{7}$$

where a_ν and b_ν are the real and imaginary Fourier coefficients at the frequency ν. The results are given in Figure 2 by the dots, and are compared with the

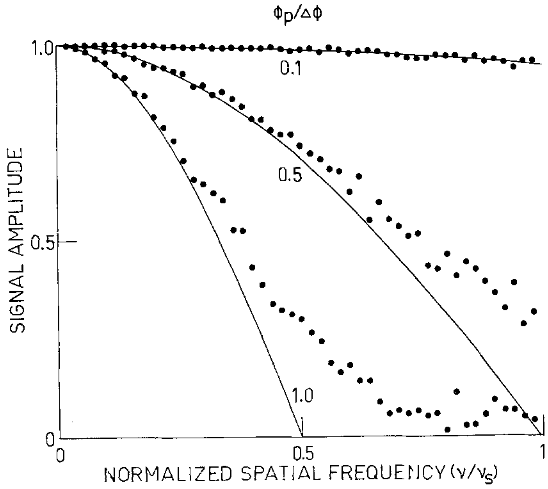

Fig. 2. The effect of irregularity on the amplitude of the observed signal for three different values of the ratio of standard deviation to mean receptor spacing. The solid lines are predictions based upon the theoretical model of (4) and the discrete points are the results of the simulation upon a finite array

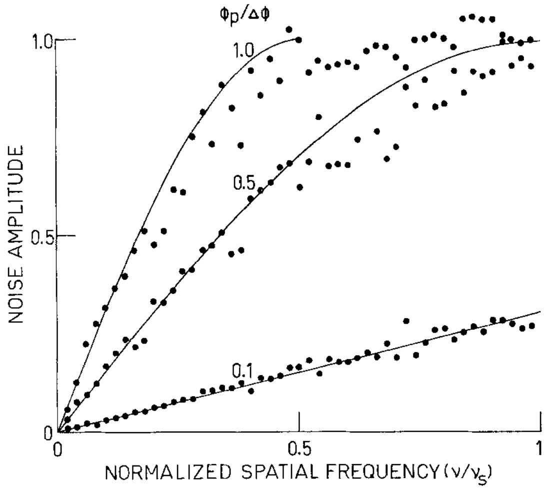

Fig. 3. The amplitude of the total background noise produced by irregular sampling for the same three cases as for Figure 2. The solid lines represent the theoretical model of (5) and the discrete points are the results of the simulation

theoretical prediction for the amplitude in the case of the infinite array [Eq. (4)]. Correspondence between the results for the two cases is good at small perturbations but becomes poorer for larger deviations near to the sampling frequency.

In addition to the signal amplitude we computed the corresponding noise amplitudes. From the simulation this was found to have a flat distribution of power at all frequencies. No tendency for power to leak sideways along the spectrum from the input frequency was observed. Thus to the observed signal a white background noise has been added. For each of the simulations the total power at all spatial frequencies other than the input was summed together and used to compute the noise amplitude. The results as functions of the spatial frequency of the input signal are plotted in Figure 3 and are compared with the theoretical prediction of (5).

The results for the signal and noise amplitudes obtained from the simulations were used to obtain signal to noise ratios for each spatial frequency and standard deviation of the perturbation. These results are plotted in Figure 4 and are again compared with the theoretical results of (6). The correspondence between the simulation and theoretical results is good in both figures for small values of the product $\nu\phi_p$.

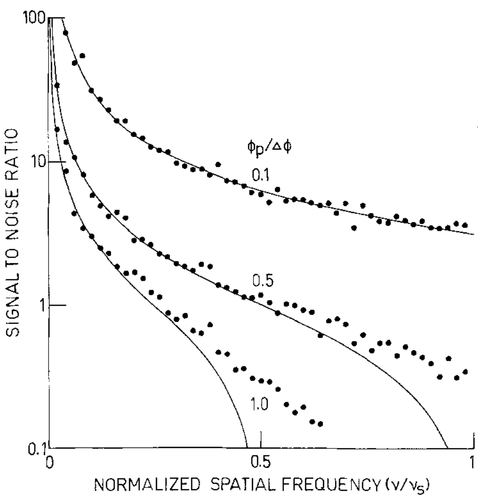

Fig. 4. The signal to noise ratio produced by irregular sampling for the same three cases as Figure 2. The solid lines represent the theoretical model of (6) and the discrete points are the results of the simulation

Discussion

In processing a spatially modulated light pattern an irregular retinal array has two detrimental effects. First, there is a frequency dependent reduction in signal amplitude (Fig. 2). Second, there is a degradation of the signal by the addition of background noise which is also frequency dependent (Fig. 3).

In both the derivation of the theoretical results and in performing the simulations we have assumed that the signal obtained from the retina is processed as if it had been obtained from a regular array. In principle it is possible to recover a signal from a perturbed array of detectors if the perturbations of the individual detectors are known (Yen, 1956; Beutler, 1970). For a visual system this would require that the central nervous system have some compensatory mechanism for processing the signals from the samplers. Although this is a possibility it seems to be unlikely. It may be rather expected that variations in the processing of the signals projected into the higher order neuron layers are statistically independent from perturbations in the photoreceptor array. Such variations will have similar effects to those discussed above, i.e. a further loss in signal amplitude and an increase in noise amplitude.

The models which we have considered are unidimensional but can be directly extended to the two-dimensional case (Snyder and Miller, 1977; Snyder, 1977). For example: we need only replace $\Delta\phi$ by $\Delta\phi\sqrt{3}/2$ in the above analysis for it to apply to a hexagonal array. Although we have used a gaussian perturbation as a reasonable first approximation to irregular sampling arrays it is probable that real retinas have more complex irregularities. In particular they are liable to exhibit a serial correlation in perturbation between samplers due to close packing of cells within an array.

Signals with spatial frequency components above the sampling frequency of the array would theoretically cause aliasing problems for a visual system. However, the retinal samplers normally sample information which is band limited by the diffraction of the pupil and associated optics (Westheimer, 1972; Van Meeteren, 1974). In the fovea the retinal samplers are spaced close to the diffraction limit (Snyder and Miller, 1976) so that aliasing cannot affect information processing. However, in the peripheral area where the samplers are distributed more coarsely aliasing may occur.

We have called the frequency dependent drop in amplitude [Eq. (4), Fig. 2] the modulation transfer function of the photoreceptor array, because it describes an alteration of spatial frequency amplitudes similar to those which occur due to diffraction or imperfections in the optical parts of the eye (Westheimer, 1972; Van Meeteren, 1974). The overall behaviour of the dioptrics and the photoreceptor array is then given by the product of the respective modulation transfer functions. Another extension is the inclusion of the modulation transfer functions for higher order ganglia, which account for the convergence of photoreceptor signals onto a smaller number of bipolar and ganglion cells (see Rodieck, 1973; Snyder, 1977).

The range of perturbations which we have used in the simulations is quite broad and probably encloses the range of actual retinal irregularities. Rodieck (1973, p. 356) has discussed the possible role of photoreceptor irregularity: "Engström (1963) found that teleosts that rely heavily on vision have visual cell mosaics, whereas those that are bottom dwellers or nocturnal lack a sharply repeating visual cell mosaic. This finding suggests a functional role for the repeating pattern, but what its role might be is quite unknown." In view of our finding, that retinal disorder reduces acuity, and specifically at the higher frequencies, there is a distinct need for animals which require high acuity to evolve a very regular array. The hypothesis that a regular mosaic is a prerequisite for highly developed motion perception (Engström, 1963; Wagner, 1971) is not contradictory with the results of our analysis of static spatial information processing.

Appendices

A. Modulation Transfer in an Irregular Lattice

Consider a sinusoidal signal $e^{j2\pi\nu\phi}$ where ν is the spatial frequency and ϕ is the spatial coordinate. Now let this signal be sampled at an irregular function of distance $\phi+q(\phi)$, where $q(\phi)$ is a gaussian white noise process of standard deviation ϕ_p and zero mean. The observed signal is therefore $e^{j2\pi\nu[\phi+q(\phi)]}$ and we may define a modulation transfer function, $M(\nu,\phi)$, where:

$$\begin{aligned} M(\nu,\phi) &= \frac{e^{j2\pi\nu[\phi+q(\phi)]}}{e^{j2\pi\nu\phi}} \\ &= e^{j2\pi\nu q(\phi)} . \end{aligned} \tag{1}$$

This function defines the change in amplitude of the spatial frequency component ν at any given position ϕ. In order to obtain an average value for this change over a large distance we may compute the mean value of $M(\nu,\phi)$:

$$\overline{M(\nu,\phi_p)} = \lim_{D\to\infty} \frac{1}{D} \int_{-\frac{D}{2}}^{+\frac{D}{2}} M(\nu,\phi)\,d\phi . \tag{2}$$

This may be expanded as:

$$\overline{M(\nu,\phi_p)} = \lim_{D\to\infty} \frac{1}{D} \int_{-\frac{D}{2}}^{+\frac{D}{2}} 1 + j2\pi\nu q(\phi) - \frac{[2\pi\nu q(\phi)]^2}{2!} + \cdots d\phi . \tag{3}$$

Since $q(\phi)$ is a white gaussian process the integrals in odd powers of $q(\phi)$ are zero valued, while the integrals in even powers reduce to powers of the standard deviation ϕ_p (Wiener, 1958). Equation (3) therefore becomes:

$$\begin{aligned} \overline{M(\nu,\phi_p)} &= 1 - \frac{(2\pi\nu\phi_p)^2}{2!} + \frac{(2\pi\nu\phi_p)^4}{4!} \cdots \\ &= \cos(2\pi\nu\phi_p) . \end{aligned} \tag{4}$$

This result implies that with zero standard deviation (regular sampling) or with zero spatial frequency (constant light intensity) the signal is recovered unattenuated. With increase in standard deviation of the random perturbation or increase in spatial frequency of the signal the attenuation increases.

B. The Variance of a Perturbed Sinusoid

We are concerned with the spatial sinusoid $x(\phi)$, where:

$$x(\phi) = e^{j2\pi\nu\phi} \tag{1}$$

and the variables are as defined above.

The mean, variance and higher order moments of the function $x(\phi)$ may be obtained from the probability density function, $p(x)$. For the case of a sinusoid the probability density function is given by (Newland, 1975):

$$p(x)=1/(\pi\sqrt{(1-x)^2}). \tag{2}$$

From this definition it may be shown that the mean is zero and the variance is $\frac{1}{2}$.

For the case of a randomly perturbed sinusoid, where the perturbation is gaussian with zero mean, the probability of finding the independent variable, ϕ, in a finite region of the spatial dimension, $d\phi$, is still given by $d\phi/S$, where S is the total distance observed. Since $x(\phi)$ is still defined by (1) the probability of finding the dependent variable, x, in a space dx is still defined in (2). It follows that the mean and total variance of the perturbed signal are identical to those of the original signal.

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Dr. A. S. French
Dept. of Physiology
University of Alberta
Edmonton, Alberta T6G 2EI, Canada